Agricultural and Forest Entomology (2000) **2**, 203–215

Spider abundance and diversity in apple orchards under three insect pest management programmes in Washington State, U.S.A.

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Abstract

1 Many apple growers in Washington State, U.S.A. use mating disruption (MD) for control of codling moth, *Cydia pomonella* (Linnaeus). Fewer applications of synthetic, broad-spectrum insecticides are made in MD orchards than in orchards under conventional (C) management. Spider abundance and diversity in MD, C and certified organic (O) orchards were compared. Spiders inhabiting the trees (arboreal), the understory vegetation, and the ground surface were studied.

2 Total arboreal spider density and total understory spider density were significantly higher in O orchards than in MD and C orchards. Many species occurred in both the trees and the understory.

3 Arboreal, visually orientated, hunting spiders and arboreal ambushers/runners were significantly more abundant in O orchards compared to C and MD orchards. Visual hunters were significantly more abundant in MD compared to C orchards. Numbers of spiders in two other guilds (web-makers and nocturnal hunters) showed no statistical differences with respect to orchard management type.

4 The highest density of ground surface-dwelling spiders occurred in one of the O orchards. Two C orchards had higher densities than any MD orchard. Ground surface species were distinct from those in the understory and the trees.

5 With one exception, an orchard's arboreal fauna was most similar to that of another orchard under the same type of pest management. Three exceptions were noted among comparisons of the understory faunas. The ground surface-dwelling fauna of one O orchard was distinctive, whereas that in the second O orchard was similar to the C and MD orchards.

6 Reduced use of synthetic, broad-spectrum insecticides in MD orchards did not result in arboreal spider densities comparable to those found in O orchards. A contributing factor may be that all species were univoltine. Spider populations may thus be severely reduced by even a small number of synthetic, broad-spectrum insecticide applications and the time required for recovery may be lengthy.

Keywords Apples, Araneae, mating disruption, natural enemies, orchards, pest management, spiders.

Introduction

Spiders are found in most terrestrial habitats and are often present in high numbers (Kaston, 1978). All spiders are predaceous and insects comprise their primary prey (Turnbull, 1973). Despite these facts, Debach & Rosen (1991) noted that spiders have been neglected as potential biological control agents and attributed this in part to their generalist predatory habits. Reichert & Lockley (1984) and Marc & Canard (1997), however, emphasized the contribution of the spider community as a whole to insect control in agroecosystems. They recognized that the diverse prey capture strategies and microhabitat exploitation of different species would exert predation pressure on a variety of pests and different life stages of the same pest. Both argued strongly for preservation of spider diversity in agroecosystems.

The role of spiders in the regulation of orchard pest insect populations has been of interest for several decades. Pickett *et al.* (1946) advocated an ecological approach to pest management

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that considered the role of natural enemies. Since then, a number of studies have investigated spiders on apples and other tree fruits. Chant (1956) and Dondale (1956, 1958) were among the first, and studied the spider faunas of apple orchards in England and Nova Scotia, Canada, respectively. Subsequently, orchard-inhabiting spiders have attracted the attention of workers in various parts of the world, including Australia (Dondale, 1966), Israel (Mansour *et al*., 1980), Italy (Angeli *et al*., 1996), Canada (Dondale *et al*., 1979) and the United States (Legner & Oatman, 1964; McCaffrey & Horsburgh, 1980; Wisniewska & Prokopy, 1997).

The detrimental impact of synthetic, broad-spectrum insecticide use on spider abundance and diversity has been clearly demonstrated. Compared to those receiving little or no such insecticide input, orchards under conventional insecticide spray programmes have lower spider populations and fewer species (Chant, 1956; Legner & Oatman, 1964; Mansour *et al*., 1980). Codling moth, *Cydia pomonella* Linnaeus, is the principal insect pest of apples in central Washington. Tolerance for its presence in the fruit is low and apple pest management tends to revolve around control of this insect. Codling moth control in conventional orchards is typically achieved with two to six applications of insecticides. Azinphosmethyl, an organophosphate, has been the insecticide of choice for many years. Treatments for secondary pests are applied as needed.

An estimated 15 000 ha of apples in Washington were treated with mating disruption (MD) technology in 1998 to control codling moth. Fewer applications of synthetic, broad-spectrum insecticides are made in MD orchards to control this pest. Mating disruption and other techniques less reliant on pesticides are certain to increase in the United States because of the federal Food Quality Protection Act. Consequently, the United States Department of Agriculture Agricultural Research Service has sponsored a series of Codling Moth Areawide Management Projects in the western states. Initiated in 1995 as 5-year programmes, they were designed to show the feasibility of MD on large areas involving several cooperating growers.

Reduced insecticide use in MD orchards may benefit natural enemies and one of our objectives was to compare spider densities in mating disruption (MD) orchards, conventional (C) orchards, and orchards under organic (O) management, where synthetic insecticides are not used. Some previous studies indicated that insecticides affect spiders more or less severely depending on the prey capture guild to which they belong (Specht & Dondale, 1960; Mansour *et al*., 1980; Bostanian *et al*., 1984). If insecticides affect spiders in certain prey capture guilds more severely than spiders in other guilds, the composition of the spider fauna in orchards under different management programmes may be quite different. We were thus interested in documenting differences, if any, in prey capture guild structure among orchards under the three management programmes and in determining which orchards had the most similar spider faunas.

Materials and Methods

Study sites

Nine orchards were sampled. Pest management programmes were set by the individual growers, thus we could not allocate treatments randomly among the orchards when selecting study sites. This led to potential statistical concerns, which we address below (see Analyses). The orchards are located in Yakima County, Washington in the south-central part of the state. The Parker Heights Areawide Project orchards are located just south-east of the cities of Yakima/Union Gap in the Yakima Valley. The project originally consisted of 162 largely contiguous hectares of apples and 40.5 ha of pears owned by seven growers. Mating disruption began in 1995, but all project orchards also received one and a half to five azinphosmethyl cover sprays to lower codling moth populations. During 1996, 1997 and 1998, cover sprays were reduced to about one per orchard per season. Secondary pest control continued as needed. For example, chlorpyrifos, an organophosphate, was applied in many orchards to control leafrollers.

Three mating disruption orchards (MD1, MD2, MD3) were monitored. Red Delicious was the principal variety in MD1 and MD3, and Golden Delicious in MD2. The northern and eastern edges of MD1, a 3 ha block, bordered uncultivated ground, largely sagebrush (*Artemisia* spp.; Asteraceae) steppe, but was otherwise bounded by orchards. MD2 (4 ha), 250 m south of MD1, was surrounded by apples and pears. The nearest uncultivated ground was 275 m to the east. MD3 (4 ha) was part of a 40 ha orchard 0.6 km east of the other project orchards, which was entirely surrounded by sagebrush steppe. MD3 was located at the eastern end of this large orchard and 60% of its edge bordered sagebrush steppe, the remaining 40% other apples. Understory vegetation in all blocks was dominated by grass, with variable intermixtures of broadleaf species. The understory was mowed at irregular intervals, but not more frequently than every 5–6 weeks, and reached 0.5 m or more in height between mowings. All orchards were irrigated with sprinklers set 0.5 m above ground, referred to as below-canopy irrigation.

Three conventional (C) orchards, owned by cooperating growers, were monitored. They received four to six codling moth cover sprays per season in addition to sprays for secondary pests. C1 (0.5 ha) and C3 (1 ha) were Golden Delicious blocks, whereas C2 (4 ha) was 75% Red and 25% Golden. C1, 8.5 km south-east of the MD blocks, was surrounded by other orchards, and was more than 1 km from the nearest native vegetation. C2, 6 km south-east of the MD blocks was bordered on three sides by cropland (primarily orchards) and on the fourth by a narrow strip of disturbed ground along a railroad. The nearest native habitat was 0.5 km away. C3, 2.5 km south-east of the MD orchards, was surrounded by other orchards, and was 100 m from uncultivated, sagebrush steppe to the north. C1 and C3 consisted of large trees with closed canopies and sparse understory vegetation. Because of this it was difficult to obtain regular sweep samples (see below) in these two blocks. Understory vegetation in C2 was similar in composition and structure to that in the MD blocks. Mowing schedules in C orchards were similar to those in MD orchards and all three were below-canopy irrigated.

Organic (O) orchards were the third type monitored but were not part of the Parker Heights Areawide Project. Organic orchards in Washington are state certified and follow strict guidelines for control of arthropods, weeds, pathogens and vertebrates. Synthetic insecticides such as organophosphates and carbamates may not be applied. Conventional orchards may be converted to organic management via a 3-year transition programme.

Organic block O1, 10 km north-east of the MD orchards, had been under organic management for 10 years. This 12 ha block consisted of six rows of Red Delicious alternating with two rows of Golden Delicious. It was bounded to the south and north-east by orchards, to the west by pasture, and to the north-west and east by uncultivated but disturbed ground. The nearest native vegetation was 1 km away. Understory vegetation was dominated by grass but also included broadleaf species. O1 was mowed less frequently than any of the other orchards and was irrigated below the canopy.

Organic blocks O2 and O3 were located 17 km east-south-east of the MD orchards and were owned by the same grower. They had been under organic management for 8 years. O2 (6.5 ha) consisted of two rows of Golden Delicious alternating with eight rows of Red Delicious and irrigation was below-canopy. This block was surrounded by other orchards and the nearest native vegetation (sagebrush steppe) was 125 m away. O3 (3.4 ha), 115 m north of O2, was a mixture of Red and Golden Delicious and was the only orchard irrigated with sprinklers set above the tree canopy. Trees in this block were older and larger than in O2. O3 was surrounded by orchards, but its south-east corner was within 35 m of sagebrush steppe. Understory vegetation in both blocks was dominated by grass with intermixed broadleaf species. O2 and O3 were mowed at 5–6 week (occasionally longer) intervals.

Sampling

Arboreal spiders were sampled with a rectangular (0.45 m^2), canvas, beating tray (Bioquip products; Gardena, CA). The tray was held beneath a branch, which was struck sharply three times with a stiff rubber hose (35–40 cm long). Branches were 1–2 m above ground. Dislodged spiders were collected from the tray with an aspirator, and preserved in 70% alcohol or saved for rearing. One branch on each of 25 trees was sampled while walking a circuit so as to include all parts of the orchard. Branches were chosen to be as uniform as possible given variability in tree size, age and pruning pattern. Different trees were sampled on each sample date. Samples were collected at 1–2 week (occasionally longer) intervals from 11 June to 7 November 1996 and 23 March to 25 October 1997. During 1998, blocks MD3, O1, O2 and O3 were sampled from 29 March until 24 October. Sampling was conducted between 09.00 and 15.00 hours.

Spiders inhabiting the understory vegetation were sampled with a 38 cm diameter sweep net. Twenty-five 180° sweeps were taken per sample while walking a circuitous route through the orchard. Net contents were emptied onto a cloth sheet and spiders collected for preservation or rearing. The tallest, densest vegetation in the orchard was swept. Samples were taken from 21 June to 1 November 1996 and from 16 May to 21 October 1997 at variable intervals depending upon mowing, irrigation and insecticide applications.

Ground surface-dwelling spiders were sampled with pitfall traps. A 16 cm length of polyvinyl chloride pipe was placed in a vertical hole in the soil so its top was level with the surface. A plastic cup (237 mL, 7 cm diameter) containing 75–100 mL of propylene glycol (Sierra® brand antifreeze) preservative was placed in the top of the pipe. A 20 cm × 20 cm plywood square was suspended 5 cm above each trap with nails to keep out water and debris. Each of six traps was placed 60–90 cm from the base of a tree in a central row of each orchard. Traps were spaced evenly along the tree row. Traps were changed at 3-week intervals. Nine consecutive collections were made from 11 April to 13 September 1997. Pitfall traps were not run in O3.

Spider identification

Spiders were identified to species, if possible, using available keys. Assistance was provided by specialists (see Acknowledgements). Because species identification requires adults, representative immatures were reared. Small spiders were housed in 34 mL plastic cups with plastic lids. Large spiders were kept in Petri dishes. Spiders were fed field-captured and laboratory-reared insects of appropriate size and small drops of water were provided as needed.

Spider prey capture strategies are diverse (Nyffeler *et al.*, 1994) and some previous studies have noted differences in the spider faunas of sprayed and unsprayed orchards based on prey capture strategy (see Introduction). For some analyses of beat tray and sweep net samples (see below) we separated spiders into four guilds based upon prey capture strategy (Wisniewska & Prokopy, 1997): visual hunters, nocturnal hunters, ambushers and runners, and web-builders (see Appendix for species list and associated guilds). Note that nocturnal hunters may not be effectively sampled by beat tray (Putman, 1967; McCaffrey *et al.*, 1984), and this guild was indeed poorly represented in our samples.

Analyses

Effects of management programme (organic, mating disruption, conventional) and year (1996, 1997) on mean, season-long densities were determined using a repeated measures analysis of variance (ANOVA), with year included as the repeated factor. Densities were expressed as the total number of spiders collected during the season divided by the number of sample dates. The number of sample dates differed among orchards because irrigation or insecticide applications prevented access to some orchards on certain dates. Separate analyses were conducted for the two sampling methods (beat trays, sweep nets). We did not analyse pitfall data statistically due to incomplete samples in block O2 caused by rodent destruction of traps and absence of traps in O3.

Two, single d.f. contrasts were defined to test the following questions. (1) Do mean spider densities in C and MD orchards differ from mean densities in O orchards? This compares orchards receiving some level of synthetic, broad-spectrum insecticide with orchards not receiving such chemicals. (2) Do mean spider densities in C orchards differ from those in MD orchards? This compares orchards receiving a high level of synthetic, broad-spectrum insecticide with those receiving a reduced level.

A second objective was to determine whether prey capture guilds differed in their numerical response to different orchard management programmes. Spiders were categorized as to guild membership, and seasonal mean guild densities were used in the analyses. Densities were compared among management programme, guild and year using a three-factor ANOVA having repeated measures for guild and year (the Case I design in Winer, 1971; p. 539–559). The between-subjects (= orchards) factor is management programme, having three levels. Separate analyses were done for beat trays and sweep nets.

We conducted univariate analyses, and present Greenhouse–Geisser adjusted P-statistics for within-subjects factors due to concerns about meeting homogeneity assumptions (Winer, 1971; p. 523). Much of our interest was with significance of the orchard type–guild interaction, as a significant interaction would imply that spiders from different guilds reacted differently to the type of orchard management system. If this interaction was significant, we tested simple effects of orchard type (Winer, 1971; p. 544–545) to determine separately for each guild whether management type affected density of that guild. Sums of squares and degrees of freedom for these tests were calculated using methods provided in Winer (1971; p. 544–545). If a specific guild was affected significantly by orchard management type, we then extracted the two *a priori* defined contrasts summarized above.

As noted above, lack of randomization of treatments among orchards led to some statistical concerns. Our major difficulty was in finding three organic orchards to include in the study. We were forced to use two orchards (O2 and O3) that were separated by only 115 m, and thus were not likely to provide independent observations. To address this concern, we first ran all of the analyses using O2 and O3 as if they were independent sites. We then re-ran each analysis after first averaging the results for these two sites (i.e., lowering replications from three to two for the organic treatment). In general, our statistical tests led to the same interpretation for the two types of analyses. In those cases in which results of the tests differed, we present both sets of statistics. Also, the organic blocks were some distance (10–17 km) from the C and MD blocks. Thus it must be noted that significant treatment effects (i.e., pest management programme) in the analyses potentially include confounding geography effects.

Similarity/dissimilarity of the spider communities between pairs of orchards was estimated by calculating a distance, or dissimilarity, coefficient, the relative absolute distance (RAD). As defined in Ludwig & Reynolds (1988)

$$\mathrm{RAD}_{jk} = \sum_{i=1}^{S} \left| \left(\frac{X_{ij}}{\sum_i^s X_{ij}} \right) - \left(\frac{X_{ik}}{\sum_i^s X_{ik}} \right) \right|$$

where j and k are the two orchards, X_{ij} is the abundance of the ith species in orchard j, and X_{ik} is the abundance of the ith species in orchard k. RAD values vary between 0 and 2, with 0 indicating the two orchards are identical and 2 indicating maximum dissimilarity. Separate comparisons were made for spiders taken by each of the three sampling methods. Beat tray and sweep net data for 1996 and 1997 were combined for these analyses, which were based on number of individuals for each species with two exceptions. (1) *Phidippus* spp. were lumped into one category because the early instars could not be distinguished with certainty. (2) Immature linyphiids, except *Meioneta fillmorana* (Chamberlin), could not be identified with certainty to species or genus and were included in the analysis as 'immature linyphiids'.

Neighbour-joining, a procedure for reconstructing phylogenies from genetic distance data (Avise, 1994), was used to generate branching diagrams which graphically represent the similarity/dissimilarity relationships among the orchards' spider faunas. RAD values were substituted for genetic distance values and orchards took the place of operational taxonomic units. Branching diagrams were generated for the aboreal, understory and ground faunas. Distance between two orchards, measured along the branching diagram, approximates the actual RAD value between the orchards (branch lengths are not strictly additive). RAD data were analysed with the Clustering Calculator program of John Brzustowski (University of Alberta) and the branching diagrams rendered by Tree View v.1.5.2, developed by Roderic D. M. Page. Both are available at www.biology.ualberta.ca/jbrzusto/cluster.html.

Results

Seasonal trends in spider densities

There were large differences among and within orchard types in arboreal spider densities in all three years (Figs 1–3). Densities were lowest in C orchards and it was not unusual to collect five or fewer spiders in a sample. No spiders were taken in C1 on seven of 15 sample dates in 1997, for example. Spider densities in MD1 and MD2 were similar to those in the C blocks. They were slightly higher in 1996 but nearly the same in 1997, when seasonal means for MD1, MD2, and C2 (the C block with the highest density) were 7.1, 7.5 and 7.2, respectively. MD3, however, had densities substantially higher than MD1, MD2, the C orchards, and organic block O1. Spider density in O1 was greater than in MD1, MD2 and the C blocks. Blocks O2 and O3 had the highest densities throughout the study.

Two patterns in spider seasonal abundance were discerned among the nine orchards (Figs 1–3). This was apparent during 1997 (Fig. 2) when sampling began earlier and a more complete seasonal picture was obtained. Spider numbers in MD and O blocks showed distinct peaks in mid- to late May and small peaks were discerned in the C blocks, although they occurred somewhat later. The peaks were attributable to the appearance of large numbers of immature *Meioneta fillmorana*. Thereafter, this species declined steadily in all orchards, and spider numbers in C and MD blocks never again approached those observed during May–June. Spider numbers in O1 remained fairly constant as late as mid-October. O2 and O3, however, showed a different pattern during the second half of the season. Densities in O2 and O3 declined after the May–June peak, began to climb from mid-July onward, and reached their highest levels of the season in August–September. The species primarily responsible for this seasonal trend was the jumping spider, *Pelegrina aeneola* (Curtis) (Salticidae), recently hatched young of which began to appear in late June. This species was the most common spider in the three organic orchards but was undetected in the C and MD blocks. Other species that contributed to high spider numbers in O2 and O3 during the latter half of the season were *Theridion neomexicanum* Banks (Theridiidae), *Oxyopes sca-*

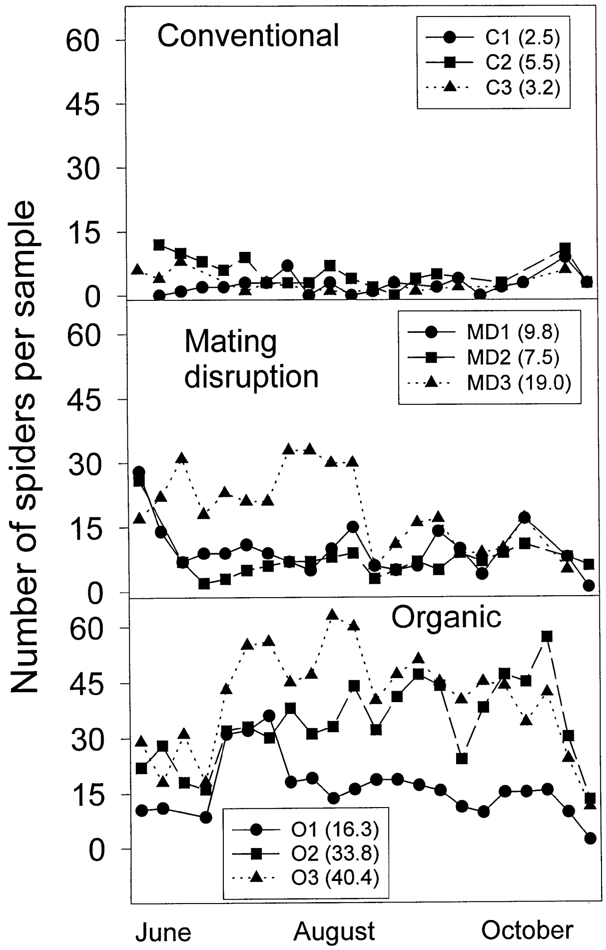

Figure 1 Number of arboreal spiders per 1996 beating tray sample. Season long mean for each orchard in parentheses. (mean ± SE: O blocks = 30.1 ± 4.6; MD blocks = 12.1 ± 4.6; C blocks = 3.7 ± 4.6).

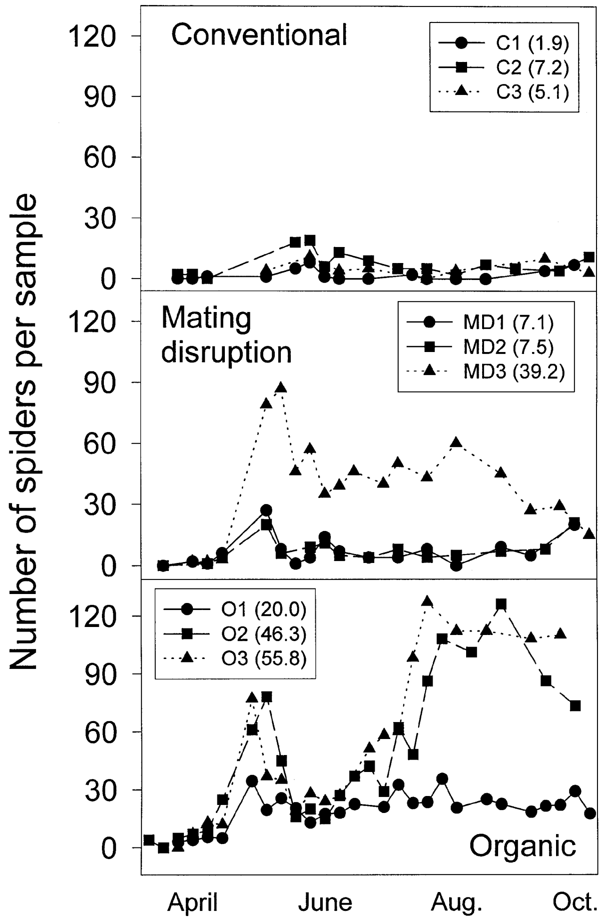

Figure 2 Number of arboreal spiders per 1997 beating tray sample. Season-long mean for each orchard in parentheses. (mean ± SE: O blocks = 40.7 ± 8.8; MD blocks = 17.9 ± 8.8; C blocks = 4.7 ± 8.8).

laris Hentz (Oxyopidae) and *Philodromus cespitum* (Walckenaer) (Philodromidae). Recent hatchlings of all three appeared during this time. *Oxyopes scalaris* was also abundant in MD3, where it was the most common species during August.

Density trends during 1998 in MD3 and the O orchards (Fig. 3) were similar to those in 1997. A peak during the second half of May was followed by a steady decline, again largely attributable to *M. fillmorana*. Densities in MD3 and O1 never again approached early season levels, whereas densities in O2 and O3 climbed steadily through July and reached their highest levels in August and September. The same four species as in 1997 were responsible for the bulk of the increase.

In 1996, sampling did not begin until June (Fig. 1), and the May–June *M. fillmorana* peak was largely missed. However, the first sample (11 June) from MD1 and MD2, in each case the highest of the season, yielded 25 *M. fillmorana* out of 28 spiders in MD1 and 22 out of 26 in MD2. Numbers in both blocks then dropped, corresponding to similar declines observed the next 2 years. Spider densities in O2 and O3 rose during July and remained high until the late season decline, as they would in 1997 and 1998.

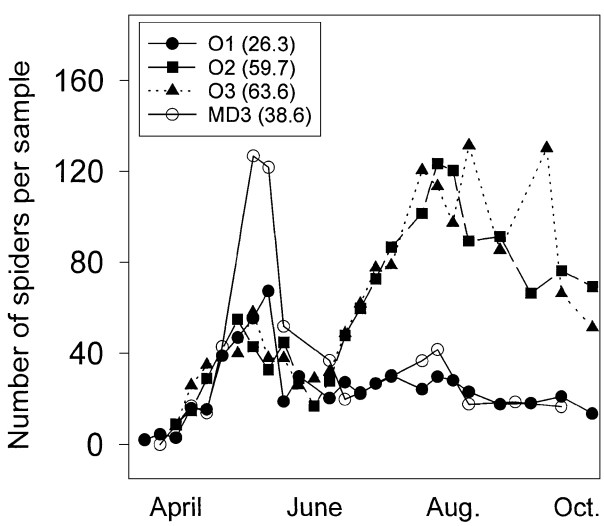

Figure 3 Number of arboreal spiders per 1998 beating tray sample for the four orchards sampled season-long. Season-long mean for each orchard in parentheses.

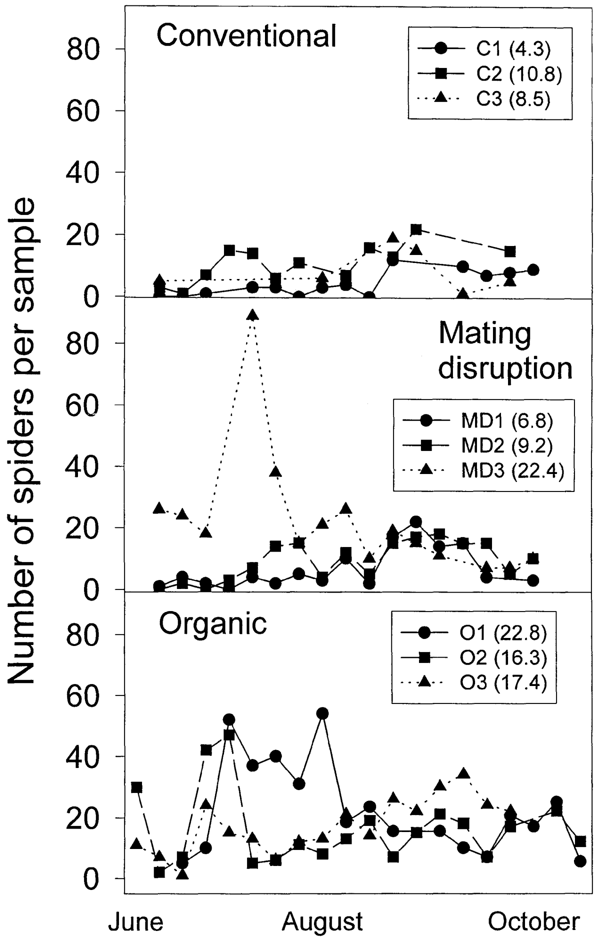

Figure 4 Number of cover crop spiders per 1996 sweep net sample. Season-long mean for each orchard in parentheses. (mean ± SE: O blocks = 18.8 ± 3.5; MD blocks = 12.8 ± 3.5; C blocks = 7.9 ± 3.5).

Season-long densities of arboreal spiders were significantly higher in organic orchards than in the C and MD orchards (by single d.f. contrast: $F_{1,6} = 12.6$, $P = 0.012$ [$P = 0.048$ if O2 and O3 first pooled]). The reduced pesticide use in MD orchards, however, did not result in significantly higher densities compared to those occurring in C orchards ($F_{1,6} = 2.8$, $P = 0.14$). Densities were similar between years ($F_{1,6} = 3.8$, $P = 0.10$).

Understory spider densities also showed considerable variation among and between orchard types (Figs 4 and 5). MD1, MD2 and the C blocks had the lowest densities. C2 had the highest density among these five orchards in both years, although the 1997 mean of 12.4 per sample was inflated due to the collection of 58 small, immature, linyphiids on 2 September. This sample represented more than half of the understory spiders taken in C2 during 1997. Understory spiders were most abundant in MD3 and the O blocks in both years.

Although many species occurred in both the canopy and the understory, relative abundance in the two habitats often differed. *Meioneta fillmorana* was abundant in the trees but rare in the understory, whereas *Misumenops celer* (Hentz) was relatively more abundant in the understory. A peak in spider abundance in MD3 during late July 1996 (Fig. 4) and 1997 (Fig. 5) was due to immature *M. celer*. Seventy of 89 spiders taken on 24 July 1996 were *M. celer*. The species was also abundant in O1, where it made up a large proportion of understory spiders from mid-July to mid-August 1996. Total spider numbers in O2 and O3 were fairly constant over the course of the season, with a slight upward trend in the second half. This was more distinct during 1997 and the largest collections of the season in both blocks were made after mid-August.

Densities of understory spiders were higher in organic orchards than in the combined C and MD orchards (single d.f. contrast: $F_{1,6} = 8.8$, $P = 0.025$ [$P = 0.054$ if O2 and O3 pooled]). Conventional and mating disruption orchards were similar in spider numbers ($F_{1,6} = 1.0$, $P = 0.36$). Densities in 1996 were not significantly different than those in 1997 ($F_{1,6} = 0.9$, $P = 0.39$).

Rodents destroyed the contents of many pitfall traps in O2 but were not a problem elsewhere. Ground surface-dwelling spiders were far more abundant in C orchards, relative to MD and O orchards, than they were in beat tray or sweep net samples. The mean number captured per sampling period in the C blocks (35 in C1, 64 in C2, and 23 in C3) was similar to the MD blocks (16 in MD1, 25 in MD2, and 25 in MD3). C2 was second only to O1 (79 per sample) in pitfall-captured spiders. The mean number of spiders captured per sampling period in O2, where rodents were destructive, was 16.

Composition of the ground surface fauna was similar in C and MD orchards and was dominated by several species of Linyphiidae. Linyphiids comprised 75–90% of pitfall-captured spiders in C orchards and 53–71% in MD blocks. The same linyphiid species made up 83% of O2's fauna. (This assumes that the O2 samples were representative despite destruction by rodents.) The spider fauna in O1 was markedly different from the other blocks and linyphiids made up only 10% of the total. Wolf (Lycosidae) and ground (Gnaphosidae) spiders comprised 50% and 30%, respectively, of the O1 fauna. By contrast, lycosids made up 10% to 24% of the spiders in C orchards and 16% to 34% in MD blocks. *Trochosa terricola* Thorell was the principal lycosid species in all blocks, regardless of management type. Gnaphosids made up less than 5% of the trap catch in C and MD orchards. Six other families (Agelenidae, Clubionidae, Philodromidae, Salticidae, Therididae, and Thomisidae) were represented in pitfall traps. Clubionids (sac spiders) made up 8.4% of the O1 fauna, but in no other case did one of these families comprise more than 5% of an orchard's fauna.

Effects of management type on spider guilds

Visual predators and web-builders were abundant in both the tree canopy (Fig. 6) and understory (Fig. 7). Ambush predators were abundant in the understory, but relatively less common in the canopy. Nocturnal spiders were uncommon in both habitats, but may have been underrepresented owing to inadequacies of the sampling methods, especially for the arboreal habitat. The guild × orchard interaction was highly significant for the beat tray data ($F_{6,18} = 10.2$, $P = 0.003$), indicating that guilds differed in how they were affected by management programme. Summary means seem to indicate that web-builders were less affected by pesticides than were visual and ambush predators (Fig. 6: open and cross-hatched bars vs. black bars). Simple

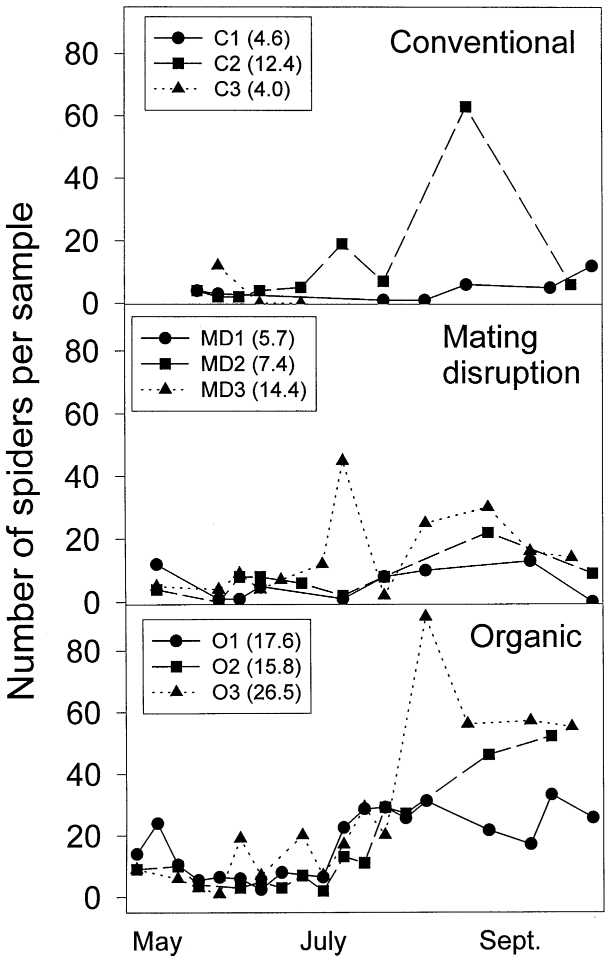

Figure 5 Number of cover crop spiders per 1997 sweep net sample. Season-long mean for each orchard in parentheses. (mean ± SE: O blocks = 20.0 ± 3.1; MD blocks = 9.2 ± 3.1; C blocks = 7.0 ± 3.1).

effects contrasts for the beat tray data showed that densities of visual predators and ambush predators were higher in O orchards than in the combined C and MD orchards (visual predators: $F_{1,12} = 54.8$, $P < 0.001$; ambush predators: $F_{1,12} = 8.1$, $P < 0.02$ [$P = 0.07$ if O2 and O3 pooled]). No such effects were noted for the other two guilds ($P > 0.10$ for both guilds). Densities of visual predators were significantly higher in MD orchards than C orchards (Fig. 6: $F_{1,12} = 5.7$, $P < 0.05$), but not if results for O2 and O3 are pooled before conducting the ANOVA.

The guild × orchard interaction was not significant for the understory results (Fig. 7: $F_{6,18} = 2.2$, $P = 0.13$), indicating that treatment effects were similar among guilds. Densities were higher in the organic than in the combined MD and C orchards ($F_{1,6} = 12.1$, $P = 0.013$); densities were not significantly different between C and MD orchards ($F_{1,6} = 2.4$, $P = 0.18$).

Community composition

Similarity relationships among orchard spider faunas are shown Fig. 8. The arboreal spider faunas of the three O orchards were similar to each other (RAD values: 0.33–0.54), but distinct from the C and MD faunas (RAD values: 1.08–1.44). This was due largely to *Pelegrina aeneola*, the dominant species in each O block, but absent in C and MD orchards. C and MD orchards were more similar to each other (RADs: 0.26–0.95) than to any of the O blocks (RADs: 1.08–1.39), owing to the greater relative contribution of *Meioneta fillmorana* to the C and MD faunas and the absence of *P. aeneola*. C and MD blocks were most similar to another orchard of the same management type, with one exception (C2 slightly more similar to MD1 and MD2 (RADs = 0.37) than to C3 (0.42) or C1 (0.56)). MD1 and MD2 were the most similar orchards (RAD = 0.26).

The understory spider fauna in each C orchard was most similar to another C orchard, and the second most similar orchard was also C in two of three comparisons. Most similar pairs of C orchards had lower RAD values (0.28–0.39) than most similar pairs of MD and O orchards (RADs: 0.39–0.92). MD1's understory fauna was most similar to C1, C2, and C3, respectively (RADs: 0.39, 0.53, 0.57), whereas MD2 was most similar to O2 (RAD = 0.50). MD3 was most similar to MD2 (RAD = 0.92) but this was the highest RAD for any most similar orchard pair, and MD3 also had the highest mean RAD (1.18) of any block. Its understory fauna was the most distinctive among the nine orchards, owing in large part to high numbers of *Misumenops celer* and *Phidippus* spp. The organic blocks were generally most similar to other O orchards but their understory faunas were less distinctive than their arboreal faunas because of lower proportions of *P. aeneola*.

The ground surface spider fauna in O1, owing to its high proportions of lycosid, gnaphosid, and clubionid spiders, was distinct from the other orchards. Its mean RAD of 1.39 was the highest value for any orchard and any of the three habitats. The C orchards and O2 had similar ground surface faunas, and for each block the other three orchards had the first, second and third most similar faunas. Each MD block was most similar to one of the other MD orchards.

Discussion

Low densities of arboreal spiders in conventional Washington apple orchards are not surprising, based on studies conducted elsewhere. Without exception, spider densities were lower where synthetic, broad-spectrum insecticide use was high compared to orchards receiving little or none (Chant, 1956; Legner & Oatman, 1964; Mansour *et al.*, 1980; McCaffrey & Horsburgh, 1980; Bostanian *et al.*, 1984). Madsen & Madsen (1982) documented a near absence of spiders in a C apple orchard where the pest complex and insect control programme were similar to those in the present study.

Arboreal spider populations in MD orchards were not significantly higher than in C blocks, despite fewer codling moth cover sprays in the MD blocks: 2.5– 3.5 azinphosmethyl sprays in 1995 but one or none in 1996 and 1997. However, insecticide use in MD orchards was not limited to azinphosmethyl. MD1 and MD2, for example, received single applications of five different materials in 1997, including chlorpyrifos, malathion, carbaryl and endosulfan for control of secondary pests. All of these products have been shown to affect spiders

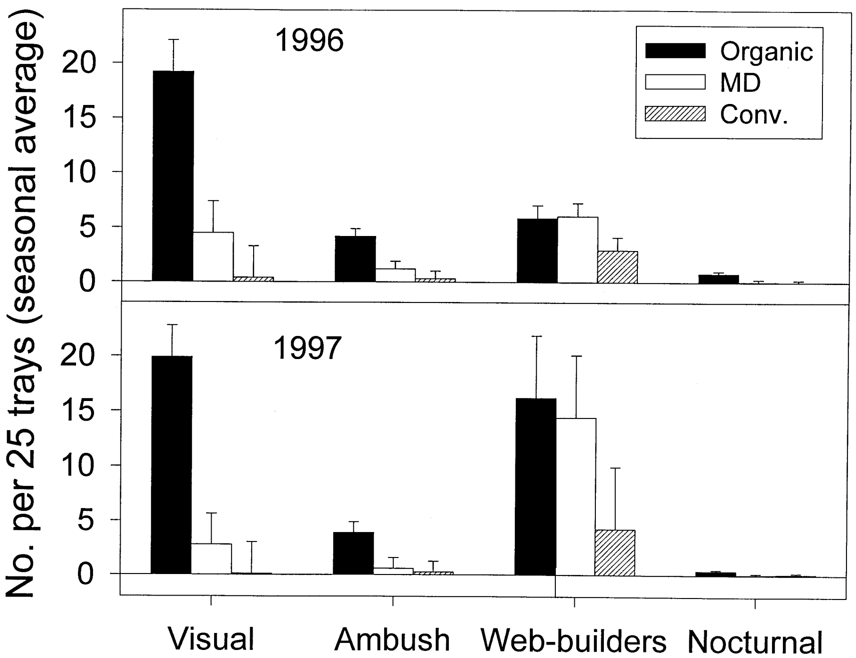

Figure 6 Seasonal mean number of arboreal spiders in each of four guilds (beating tray collections). Means based on combined data for the three orchards of each type.

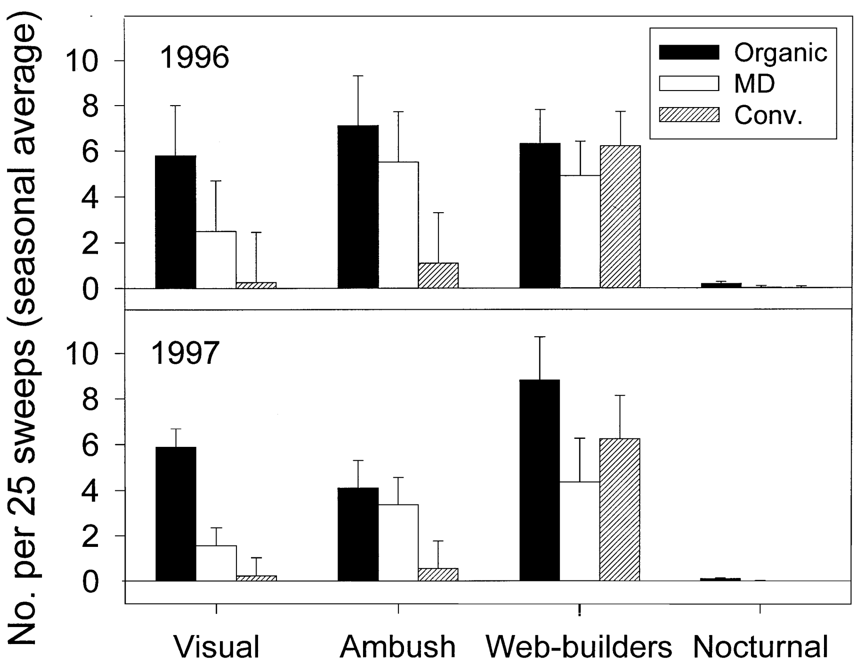

Figure 7 Seasonal mean number of cover crop spiders in each of four guilds (sweep net collections). Means based on combined data for the three orchards of each type.

negatively (Herne & Putnam, 1966; Culin & Yeargan, 1983; Mansour, 1987; Mansour & Nentwig, 1988). Continued use of broad-spectrum insecticides in MD orchards, despite the reduced number of applications, may prevent spider populations from reaching densities observed in unsprayed orchards. A significant constraint on spider population increase under such conditions may be the univoltine life cycles of most temperate-zone species (Gertsch, 1979; p 48). No species in this study

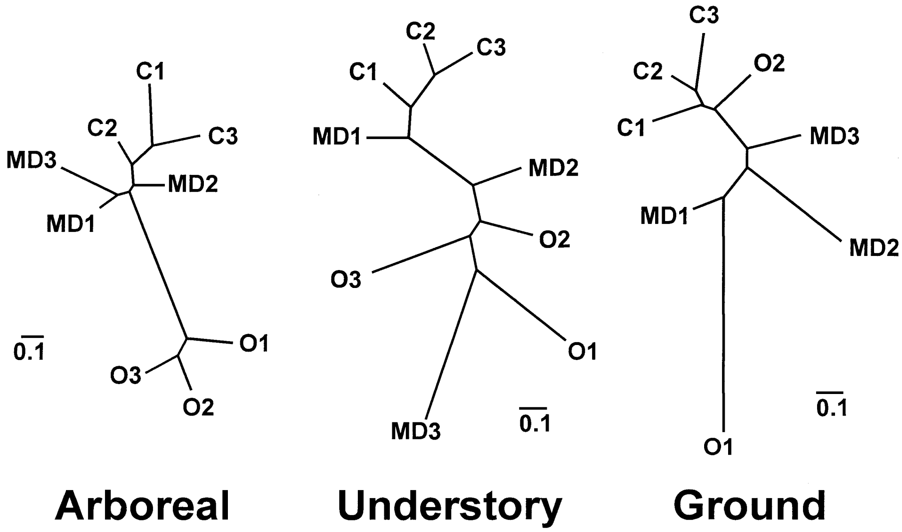

Figure 8 Branching diagrams showing similarity relationships among the orchards' spider faunas based on neighbour-joining analysis of distance (RAD) data. Distances between orchards, measured along a tree, indicate relative similarity between orchards. Distance scales differ slightly for the different diagrams.

appeared to have more than one generation per year. Each application of a toxic insecticide would reduce spider numbers and, in the absence of immigration, population recovery would not begin until the next reproductive cycle.

Immigration may help explain the high spider densities noted in MD3. This orchard was bordered by uncultivated, sagebrush steppe along 60% of its perimeter. *Oxyopes scalaris* was the second most abundant spider in MD3 and first appeared in mid-July as small immatures. By mid-October, the spiders were about half grown but the species had largely disappeared from the orchard, a pattern observed in 1996, 1997 and 1998. Adults were rarely collected in the orchards but occurred in adjacent sagebrush during May and June (unpublished data), a habitat known to be important for this species (Dondale & Redner, 1990). Immature *O. scalaris* may disperse after egg hatch and colonize orchards, persisting until late in the season. Their subsequent fate is unknown but may involve a return to sagebrush to complete development. A second important colonizing species was *Meioneta fillmorana*, the most abundant spider in MD3. Dispersal by ballooning is common in the Linyphiidae (Reichert & Lockley, 1984) and immature, although not adult, *M. fillmorana* were common on sagebrush in late April and the first part of May (unpublished data). Immigration into MD3 from adjacent sagebrush steppe could explain, in part, the high spider densities observed in this orchard compared to the other two MD blocks.

Colonization of orchards and other agroecosystems by spiders needs further study. Chant (1956) noted that the spider fauna of insecticide-treated apple orchards consisted largely of species found in adjacent habitats, whereas unsprayed blocks had a predominantly indigenous fauna. Agnew & Smith (1989), working on peanuts, an annual system, stated that spider colonization was by immigration from adjacent habitats. Bishop & Riechert (1990), however, found that many immigrants into annual garden plots were not found in adjacent habitats and had presumably arrived from a considerable distance away. They felt that the more physiognomically similar were the crop and its surrounding habitat the more likely the crop's spider fauna would be derived extensively from surrounding habitat.

Most previous studies in orchards compared spider densities in unsprayed and conventional blocks. Fewer studies have been conducted in modified or reduced spray orchards. Specht & Dondale (1960) compared modified spray (insecticides replaced by less potent ryania, nicotine bentonite and lead arsenate compounds) with unsprayed orchards. Spider densities were initially higher in the unsprayed programme but the difference decreased through the season. Wisniewska & Prokopy (1997) compared spider densities in first- and second-level IPM plots. Under second-level IPM synthetic, broad-spectrum insecticides were not applied after early June (no restrictions in first level). Spiders were two or three times more abundant in second-level IPM by season's end and were most abundant in August and September. In the present study, by contrast, C and MD spider densities were highest during late May and early June and declined over the rest of the season. The difference may be due to timing of chemical applications. Wisniewska & Prokopy (1997) felt that curtailing broad-spectrum use after early June allowed spider populations time to recover. Similar restrictions were not applied in the current study. For example, chlorpyrifos was applied on 22 August 1996 and appeared to be responsible for a substantial decrease in spiders in MD3 (see Fig. 1).

Studies have also shown that community composition changes with insecticide use. Chant (1956) identified only half as many species in sprayed as in unsprayed orchards. Specht & Dondale (1960) noted a lower proportion of hunting spiders in sprayed compared to unsprayed blocks (49% vs. 68%) and speculated that hunting forms might be more susceptible to insecticides. Likewise, Bostanian *et al*. (1984) showed that hunting spiders made up 26–41% of the fauna in six C orchards but 58% in their unsprayed block. The significantly lower proportion of visual hunters and ambushers/runners in C and MD compared to O blocks in the present study has been mentioned, but decreased abundance of hunters in sprayed compared to unsprayed orchards has not been found in all studies. McCaffrey & Horsburgh (1980) noted that species diversity in five C orchards was lower than in an abandoned orchard, but that the proportion of hunting spiders was similar to that in the abandoned block.

Spider webs may be efficient collectors of insecticide sprays (Samu *et al*., 1992); because some web-makers periodically ingest their webs, they may be at increased risk of pesticide exposure. Web-making Theridiidae were significantly less abundant in second-level IPM plots studied by Wisniewska & Prokopy (1997), compared to unsprayed plots, and they felt this could have been because the spiders consumed their webs. Mansour *et al*. (1980) found a lower proportion of web-making spiders in a sprayed compared to an unsprayed apple orchard in Israel (14% vs. 31%).

Meioneta fillmorana was the most abundant web maker in all orchards during the present study. Substantial decreases in its numbers were noted over short time spans on several occasions. For example, beat tray samples in MD3 on 27 May and 4 June 1997 yielded 82 and 43 specimens, a 48% decrease (see Fig. 2). As azinphosmethyl was applied late on 27 May the reduction was probably insecticide related. A similar decrease in MD3 occurred in 1998 (Fig. 3). No insecticides were applied in this block after 25 March 1998, however, and the reduction must have been due to other factors. *Meioneta* numbers also fluctuated widely in some of the organic orchards and causes unrelated to insecticide use must be sought. Large-scale emigration, perhaps prompted by unfavourable environmental conditions or lack of suitable prey, is a possibility.

Most studies of orchard spiders have examined only the arboreal fauna. Madsen & Madsen (1982), however, showed that spiders in the understory vegetation of a C orchard were less than 1% as abundant as in an O block. Differences in the present study were less extreme, although O blocks generally supported higher densities than C and MD blocks. Variability in structure, density and species composition of the understory, and vegetation management practices also probably contributed to differences in spider numbers. Some attempt was made to compensate for this variability by sampling where vegetation was tallest and most dense and by allowing vegetation to grow back after mowing. Agricultural practices that cause extensive habitat alteration or destruction severely disrupt spider communities (Reichert & Lockley, 1984). Mowing, tilling and herbicide use in orchards disrupt the understory and soil surface habitats. Mowing and tilling were used to manage vegetation even in the O orchards and probably had an adverse impact on spiders. Cultural practices causing comparable destruction of the arboreal habitat were not employed.

Few species were exclusive inhabitants of the trees or the understory. Most occurred in both habitats, although many showed a preference for one or the other (Appendix 1). The fact that many species were found in both habitats may reflect considerable movement between the two.

The ground surface spider fauna was distinct from the arboreal and understory faunas (see Appendix). Major taxa such as wolf (Lycosidae) and ground (Gnaphosidae) spiders were abundant on the orchard floor, but virtually absent in the understory and trees. Linyphiids were abundant in all three habitats but the family was more diverse on the orchard floor. *Halorates ksenius* (Crosby and Bishop), *Walckenaeria subspiralis* Millidge, and *Lepthyphantes tenuis* (Blackwall) were common or abundant inhabitants of the orchard floor but virtually absent in the trees and understory. *Meioneta fillmorana*, by contrast, was a dominant component of the arboreal fauna but was never taken in the pitfall traps. Unidentified, immature linyphiids were common in all three habitats.

The distinctive ground surface fauna increases total spider diversity and a diverse fauna will increase the effectiveness of spiders in pest control (Marc & Canard, 1997). Different spiders, by exploiting different habitats and employing different predatory strategies, attack pests at different times, locations, and stages in their life cycles. The more diverse an orchard's spider fauna the more likely that one or more species will find suitable prey among different pests and different life stages of the same pest. Codling moth adults might fall prey to arboreal web makers and some of the larger hunting spiders, whereas the tiny, neonate larvae, before they bore into fruit, may be vulnerable to various arboreal species. Mature larvae, in their search for cocooning sites, might fall prey to larger hunting spiders in the trees and on the ground.

The high densities of ground surface spiders in C orchards are interesting and puzzling. Mean densities in all three blocks equalled or exceeded those in the MD orchards, and C2 was exceeded only by O1. Lack of insecticide use and minimal mowing and tilling in O1 allowed development of relatively stable ground surface and understory habitats, factors undoubtedly important in promoting high spider densities. Reason(s) for the high spider densities in C orchards are unclear, however. Insecticide input was higher than in MD blocks and the sparse ground covers in C1 and C3 would have reduced any shielding effect of vegetation against insecticide deposition on the ground. Vegetation management in C and MD blocks was similar. None of these factors would appear to favour higher spider numbers in C compared to MD blocks.

Another interesting aspect of ground surface spiders was the distinctive composition of the O1 fauna. Web-makers, primarily Linyphiidae, were dominant in C and MD blocks, whereas Lycosidae, Gnaphosidae and Clubionidae (all hunters) dominated the O1 fauna. Epstein *et al*. (2000) found hunting spiders (primarily lycosids and gnaphosids) significantly more abundant in unsprayed compared to conventional orchards in a pitfall trapping study.

Species of small body size dominated the spider faunas of C and MD orchards and similar patterns have been seen elsewhere (Wisniewska & Prokopy, 1997). The Linyphiidae, most of whose members are less than 3 mm in length (Roth, 1993), was the most important family. Linyphiids were a dominant component of the fauna in all three orchard habitats and in only three of 30 collections (all in MD3–1996 beat trays 1996 and 1997 sweeps) did they comprise less than 45% of the total spiders taken for the season. In O orchards, by contrast, linyphiids made up more than 35% of the total spiders in only one of 14 collections (O2–1997 pitfall). One likely consequence of this difference in body size of spiders found in sprayed and unsprayed orchards could be in terms of impact on populations of prey insects. That is, the relative rarity of large spiders in C and MD orchards probably reduces the potential contribution of spiders to control of larger pest species, including, for example, prepupal larvae and adult codling moth.

Conventional apple orchards, where synthetic, broad-spectrum insecticide use is high year after year, have spider faunas of low density and diversity. Few spiders are likely to complete their life cycles and immigration may maintain the low populations that are present. Repopulation via immigration in intensively cultivated areas may be limited, however, because most surrounding land is also insecticide-treated. Spider faunas of organic orchards, by contrast, are more diverse and attain much higher densities. Many species complete their life cycles in organic orchards. Codling moth mating disruption has reduced the use of synthetic, broad-spectrum insecticides but not eliminated it. Spiders remain vulnerable to the reduced level of insecticide use in mating disruption orchards in part, perhaps, because most temperate species are univoltine. Once reduced to low levels, spider populations may require a lengthy period to build up. Unpublished observations from 1996 to 1999 in an orchard recently transitioned to organic management support this idea. To take full advantage of the insect control potential of these diverse and abundant predators, it will probably be necessary to minimize use of synthetic, broad-spectrum insecticides by employing selective materials and those of low toxicity to spiders.

Acknowledgements

We would like to express our sincere thanks to the growers who participated in the Parker Heights Areawide Program for allowing ready access to their orchards throughout this study. Their cooperation has been instrumental in demonstrating the feasibility of mating disruption for codling moth control and the benefits that go along with it. Organic growers Pete Garza and Scott Leach likewise made their orchards readily available for sampling and observations. Dave Epstein, graduate student in entomology at Washington State University, ran the pitfall traps during 1997. Andrew Moldenke (Oregon State University) provided assistance with spider identification. Rod Crawford, curator of arachnids at The Burke Museum of Natural History and Culture, University of Washington, was most helpful with identification of a number of species, especially those in the difficult family Linyphiidae. Tom Unruh kindly ran the neighbour-joining analysis. Daniel Mayer, Peter Landolt and two reviewers read the manuscript and offered helpful suggestions for its improvement.

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Accepted 22 May 2000

Appendix

Percent contribution of each species to the arboreal, understory, and ground surface faunas based on combined data for three orchards of each type: O = organic, MD = mating disruption, C = conventional. Numerical totals shown at bottom of table. Guild membership of each family indicated as: VH (visual hunter); NH (nocturnal hunter); AR (ambushers and runners); W (web maker).

Family	Arboreal			Understory			Ground surface		
Species	O	MD	C	O	MD	C	O	MD	C
Salticidae (VH)									
Pelegrina aeneola (Curtis)	43	0	< 1	20	0	0	< 1	0	0
P. helenae (Banks)	0	< 1	0	0	< 1	0	0	0	0
Sassacus papenhoei P & P	2	4	2	1	4	< 1	0	0	0
Phidippus spp. [1]	2	5	2	13	10	2	0	< 1	0
Eris militaris (Hentz)	< 1	0	0	< 1	0	0	0	0	0
Habronattus sp.	0	0	0	< 1	0	< 1	< 1	0	0
Unidentified	< 1	< 1	0	< 1	0	0	0	0	< 1
Oxyopidae (VH)									
Oxyopes scalaris Hentz	9	16	3	2	4	< 1	0	0	0
Thomisidae (AR)									
Xysticus cunctator Thorell	4	4	4	7	6	5	0	0	0
X. gulosus Keyserling	0	0	0	0	< 1	0	0	0	0
X. pretiosus Gertsch	0	0	0	0	0	0	< 1	0	0
Misumenops celer (Hentz)	2	2	1	13	31	5	0	< 1	0
Philodromidae (AR)									
Philodromus insperatus Schick	< 1	< 1	0	0	0	0	0	0	0
P. cespitum (Walckenaer)	5	< 1	1	2	< 1	0	0	0	0
Tibellus oblongus (Walckenaer)	< 1	< 1	1	6	3	3	< 1	0	0
Ebo pepinensis Gertsch	< 1	0	0	< 1	< 1	< 1	0	0	0
Thanatus sp.	0	0	0	< 1	0	0	0	0	0
Linyphiidae (W)									
Meioneta fillmorana (Chamberlin)	13	54	46	4	4	4	0	0	0
Erigone spp. [2]	1	1	3	2	3	6	6	12	12
Spirembolus mundus C. & I.	0	< 1	0	0	0	0	0	0	0
Walckenaeria subspiralis Millidge	< 1	0	0	0	< 1	0	2	5	4
Lepthyphantes tenuis (Blackwall)	< 1	0	< 1	0	0	0	2	4	3
L. leprosus (Ohlert)	0	0	0	0	0	0	0	0	< 1
Halorates ksenius (C. & B.)	0	0	1	0	< 1	1	5	11	43
Bathyphantes concolor (Wider)	0	0	0	0	0	0	0	< 1	0
Unidentified [3]	8	7	26	13	25	69	7	35	23
Tetragnathidae (W)									
Tetragnatha laboriosa Hentz	< 1	1	4	12	6	3	0	0	0
Araneidae (W)									
Argiope trifasciata (Forskal)	0	0	0	1	< 1	< 1	0	0	0
Araneus sp.	< 1	< 1	0	< 1	< 1	0	0	0	0
Unidentified	0	< 1	0	< 1	< 1	< 1	0	0	0

Family Species	Arboreal			Understory			Ground surface		
	O	MD	C	O	MD	C	O	MD	C
Theridiidae (W)									
Theridion neomexicanum Banks	7	4	3	2	1	1	0	0	0
Crustulina sticta (O. P.-C.)	0	0	0	0	< 1	0	0	0	0
Latrodectus hesperus C. & I.	0	0	0	0	0	0	0	< 1	0
Dictynidae (W)									
Dictyna spp. [4]	1	< 1	< 1	1	1	< 1	0	0	0
Uloboridae (W)									
Hyptiotes gertschi C. & I.	0	< 1	0	0	0	0	0	0	0
Clubionidae (NH)									
Cheiracanthium mildei L. Koch	1	< 1	< 1	< 1	0	0	0	0	0
C. inclusum (Hentz)	1	0	0	1	0	0	0	0	0
Castianeira longipalpa (Hentz)	0	0	0	< 1	0	0	4	0	0
C. alteranda Gertsch	0	0	0	0	< 1	0	0	< 1	0
Phrurotimpus borealis (Emerton)	0	0	0	0	0	0	3	2	0
Anyphaenidae (NH)									
Anyphaena pacifica (Banks)	< 1	0	< 1	< 1	0	0	0	0	0
Agelenidae (W)									
Hololena nedra C. & I.	< 1	0	0	0	0	0	0	0	0
Tegenaria agrestis (Walckenaer)	0	0	0	0	0	0	1	2	1
T. domestica (Clerck)	0	0	0	0	0	0	0	< 1	< 1
Lycosidae (AR)									
Trochosa terricola Thorell	0	0	0	0	0	0	41	12	6
Pardosa wyuta Gertsch	0	0	0	0	0	0	0	1	0
P. coloradensis Banks	0	0	0	0	0	0	< 1	0	0
Pardosa sp.	0	0	0	0	0	0	0	< 1	0
Alopecosa kochii (Keyserling)	0	0	0	0	0	0	0	< 1	0
Schizocosa sp.	0	0	0	0	0	0	< 1	0	0
Unidentified	0	< 1	< 1	0	0	0	2	10	7
Gnaphosidae (NH)									
Zelotes fratris Chamberlin	0	0	0	0	0	0	17	2	< 1
Z. puritanus Chamberlin	0	0	0	0	0	0	< 1	0	0
Drassylus depressus (Emerton)	0	0	0	0	0	0	1	0	0
D. lamprus (Chamberlin)	0	0	0	0	0	0	0	1	< 1
Drassylus sp.	0	0	0	0	0	0	< 1	0	0
Micaria pulicaria (Sundevall)	0	0	0	0	0	0	< 1	0	0
Unidentified	0	0	0	0	0	0	6	2	0
Totals	5527	1662	357	2520	898	388	859	598	1091

[1]Includes *P. clarus* Keyserling, *P. audax* (Hentz), and an undetermined species. [2]Includes *E. dentosa* O. Pickard-Cambridge and *E. aletris* Crosby & Bishop. [3]Includes > 95% immatures. [4]Includes *D. coloradensis* Chamberlin.

